Some Aspects of the Anatomy, Reproduction, and Early Development of *Cerithium nodulosum* (Bruguière) (Gastropoda, Prosobranchia)[1]

JOSEPH R. HOUBRICK[2]

ALTHOUGH MEMBERS of the prosobranch genus *Cerithium* occur in abundance throughout the warm, shallow, tropical waters of the world, little is known of their general ecology or life histories (Anderson, 1960). For the most part, only brief reports or notes have been published on the reproduction and early development of *Cerithium* species, namely *C. vulgatum* (Lo-Bianco, 1888), *C. ferrugineum* (Lebour, 1945), *C. obeliscus* (Ostergaard, 1950), *C. morus* (Natarajan, 1958), *C. atratum* (Marcus and Marcus, 1964), *C. algicola* (Davis, 1967), *C. variabile* (Raeihle, 1968), *C. stercusmuscarum* (Wolfson, 1969), and *C. litteratum* and *C. auricoma* (D'Asaro, 1970).

The evidence at hand (Sunderbrink, 1929; Risbec, 1943; Johansson, 1947, 1953, 1956; Marcus and Marcus, 1964) indicates that members of this genus are aphallic; have open, pallial, genital ducts; lay their eggs, either as a tangled mass or a flattened coil, in gelatinous strings or filaments attached to a substratum; and hatch out as planktotrophic veligers.

I wish to express my appreciation to Dr. Philip Helfrich of the Hawaii Institute of Marine Biology for his suggestion to use the Eniwetok Marine Biological Laboratory for this work.

ANATOMY

C. nodulosum is the largest species in the genus and occurs throughout the Indo-Pacific region, but not in Southern Japan or Hawaii (Demond, 1957). I studied it at Eniwetok Atoll, Marshall Islands, during August 1970, where it is moderately common on the windward reef shelves, occurring subtidally on rocky, sandy substrates just shoreward of the reef edge. A total of 16 specimens collected from Japtan Reef had a mean length of 101 mm; the population consisted of 14 females and two males with no sexual dimorphism evident in radulae, shell size, or sculpture.

Although Risbec (1943) discussed the general anatomy of *C. nodulosum*, he did not examine the pallial genital ducts in detail nor did he observe any males. Freshly dissected males which I examined had bright orange testes and their sperm ducts were packed with both eupyrene and apyrene sperm. The pallial genital ducts were open and consisted of lateral (left) and medial (right) laminae which were fused dorsally to each other and to the mantle. The closed sperm duct terminated in the pocketlike proximal portion of the pallial genital groove. This area was thick and glandular and probably functioned as a prostate. Beyond the prostate area the genital groove extended forward as a slitlike channel open to the mantle cavity. The epithelial lining of the inner walls of the laminae was thrown into small folds extending distally. These folds appeared to be somewhat glandular but not as highly developed as those of the proximal portion of the genital groove.

Ripe females had bright yellow ovaries which were filled with ova and oocytes. The oviduct (o, Fig. 1) was a closed tube leading into the proximal portion of the open pallial duct. The general morphology of the female pallial reproductive tract was found to be similar to that described for males except that the laminae were larger and more glandular with a thinner nonglandular portion along the edge of the medial lamina. The proximal end of the oviducal groove (og, Fig. 1) which constitutes the albumen gland (ag, Fig. 1) was thick and the epithelial lining of the inner walls of the laminae was somewhat flat, with little evidence

[1] Support for this work was provided by the U.S. Atomic Energy Commission through the University of Hawaii and the Eniwetok Marine Biological Laboratory. Manuscript received March 11, 1971.

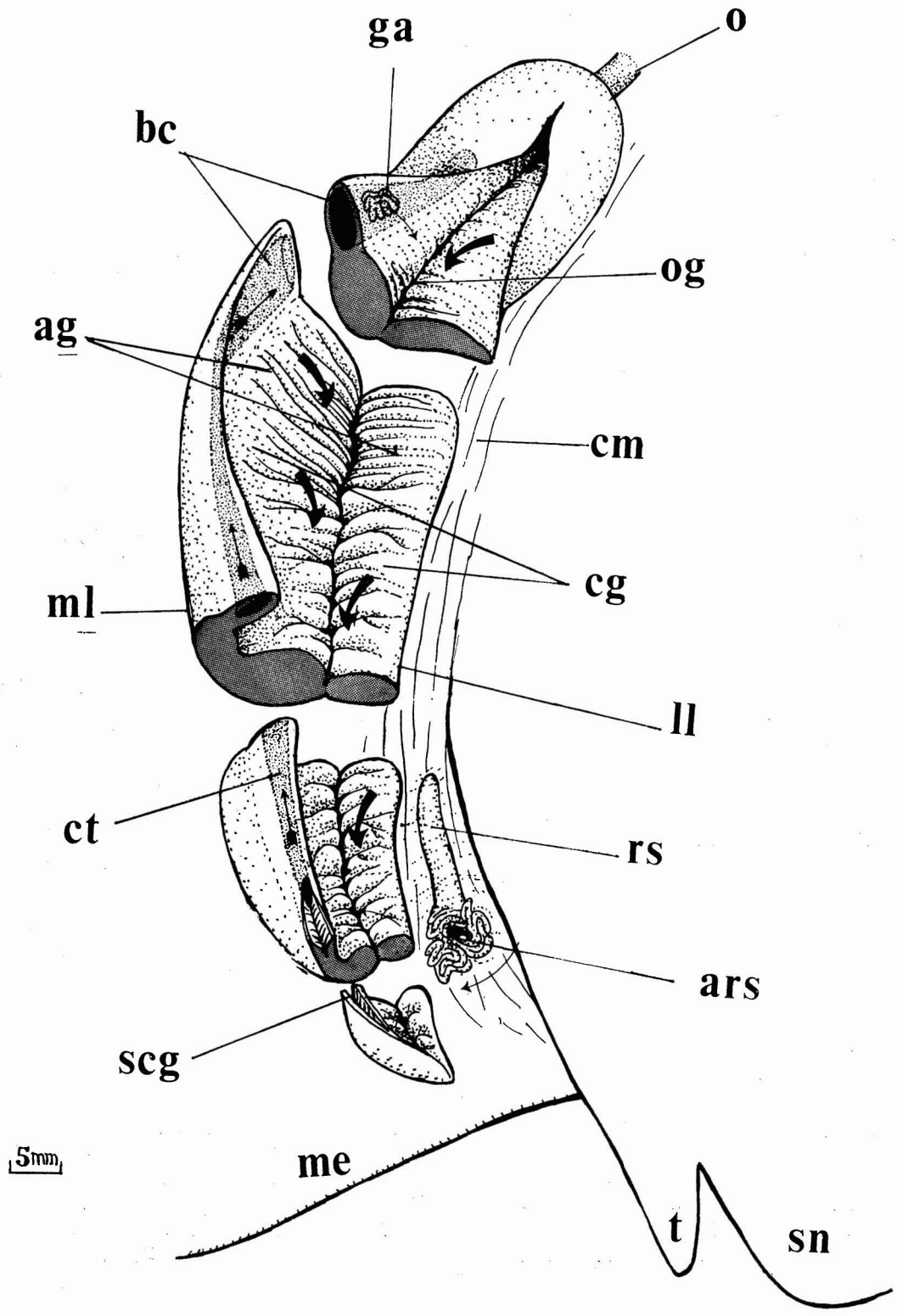
[2] Smithsonian Institution, Smithsonian Oceanographic Sorting Center, Washington, D.C. 20560.

of folds. Distal to this was a glandular medial portion of the open duct which probably functions as the capsule gland (cg, Fig. 1); here the inner walls of the laminae were glandular and folded. At the distal end of the oviducal groove on the edge of the nonglandular portion of the lamina was a short slit (scg, Fig. 1), the sperm-collecting gutter of Johansson (1953), which measured about 5 mm in length and led into the opening of a long, ciliated, flattened tube (ct, Fig. 1). This tube ran inside the entire length of the medial lamina (ml, Fig. 1) and enlarged into a chamber (bc, Fig. 1) located at its proximal end. Within this chamber were found eupyrene sperm mixed with a yellowish mucus and thin jellylike strands of unknown function. Johansson (1947) called this area in *C. vulgatum* the bursa copulatrix. Within the bursa, embedded in the wall of the inner portion of the medial lamina, was a pink glandular area (ga, Fig. 1) resembling a warty flap. Under this area a tiny opening led through the wall of the lamina into the lumen of the proximal oviducal groove (og, Fig. 1). Ciliary currents led from the bursa through the glandular area and its opening into the lumen. The unfertilized eggs left the closed oviduct in this portion of the lumen. I believe that this must be the site of fertilization, and that sperm stored in the chamber are transported through the glandular aperture into the proximal open part of the duct where they fertilize the eggs as the latter move into the open portion of the oviduct. As the fertilized eggs continue to move down the open groove, albumen and the hyaline membrane are laid down around them. At the distal end of the oviducal groove, opposite the slit on the medial lamina where the lateral lamina (ll, Fig. 1) was fused to the dorsal body wall of the animal, was situated a pink glandular area within which was an opening leading to a thin tube measuring 16 mm long and 3 mm wide. This tube was also filled with sperm and was called the receptaculum seminis by Johansson (1947) in *C. vulgatum*. It was found just beneath the epithelium. It is difficult to understand the function of a receptaculum seminis located in the distal portion of the genital duct. Eggs reaching this area would already have been encapsulated, making fertilization impossible. Moreover, there were strong ciliary currents leading from the proximal to the distal portion of the groove and it would seem impossible for the sperm to swim against such a current if they were to move from the receptaculum up to the site of fertilization. Perhaps sperm stored in the bursa are moved out of the aperture into the lumen and down the groove to the distal receptaculum seminis where they are stored. Subsequently they may leave the receptaculum seminis, be drawn into the ciliated slit, and move up into the bursa again prior to fertilization and oviposition. Thus the bursa may function as an intermediary receptaculum seminis because the sperm could then move through the aperture and fertilize the eggs before they passed through the albumen and capsule glands.

REPRODUCTION AND DEVELOPMENT

Pairing was observed in the field, but the mechanism of sperm transferral was not seen. It is no doubt similar to that process described by Fretter (1951) for *Cerithiopsis* in which sperm, liberated with prostatic fluid, are immediately drawn into the inhalent siphon of the female and thence into her mantle cavity.

One female, measuring 110 mm long and 50 mm wide, was observed depositing her egg mass. She was partially buried in the thin sand covering a limestone shelf. The crescent-shaped egg mass was attached to the rocky substrate and was also partially covered with sand. The egg mass of *Cerithium nodulosum* (Fig. 2*a*) proved to be quite distinctive in contrast to those described for other cerithiids. This egg mass consisted of a thick, ribbonlike, axial base which was of jellylike consistency. To this base were attached clusters of many coiled strings or filaments folded about themselves. The filaments were also jellylike and were covered with sand grains. The whole mass was crescent shaped and, in many respects, closely resembled that described for *Strombus* (Robertson, 1959; D'Asaro, 1965). Detached from the substrate, the basal axial position of one egg mass measured 55 mm long and 6 mm wide. Each cluster of filaments attached to this basal axial portion averaged 12 mm in length, and 33 clusters of filaments were attached to this axis. The


ga
o
bc
og
ag
cm
cg
ml
ll
ct
rs
ars
scg
5mm
me
t
sn

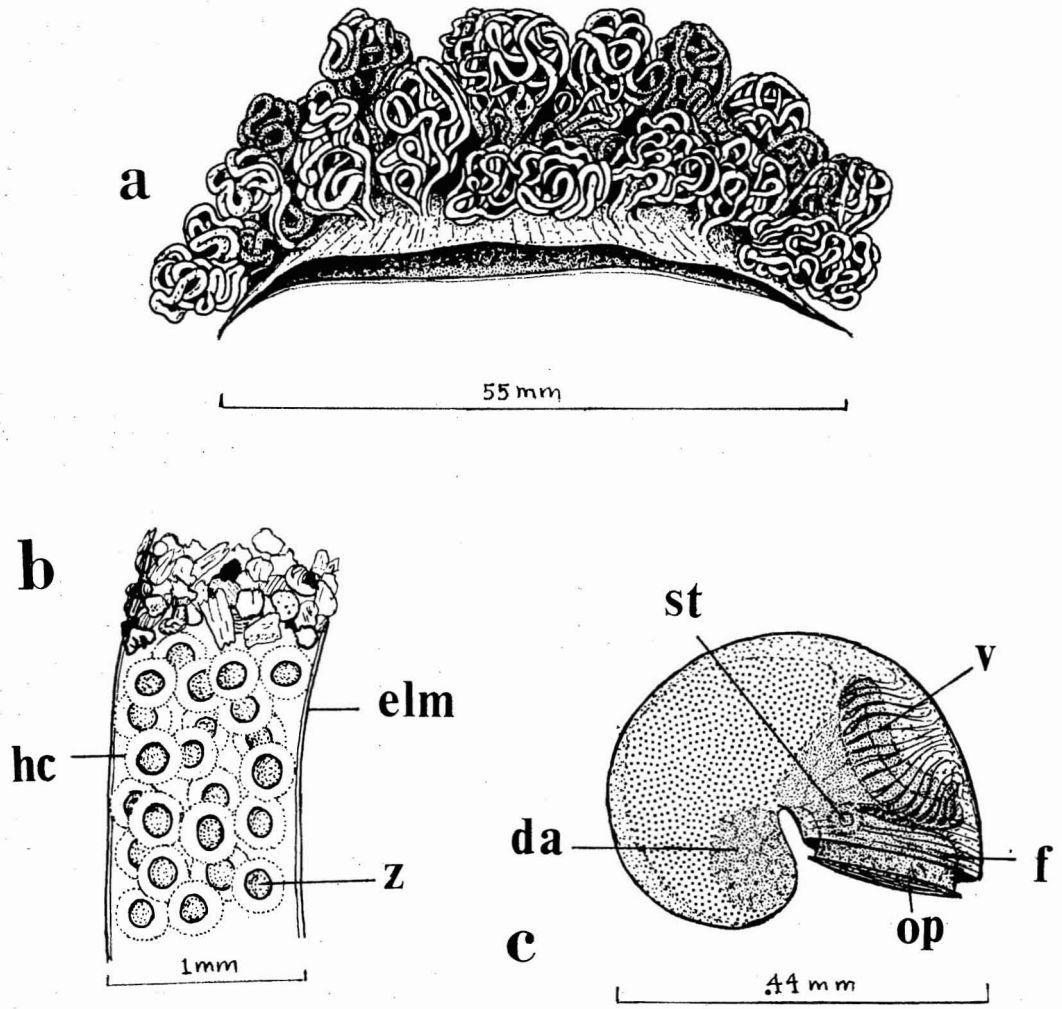


FIG. 2. *a*, Egg mass of *Cerithium nodulosum* detached from substrate and stretched to full length; *b*, portion of filament with sand grains removed to show zygotes; *c*, newly hatched veliger partially retracted in shell.

SYMBOLS: elm, external limiting membrane; hc, hyaline capsule; z, zygote; da, digestive anlage; f, foot; op, operculum; st, statocyst; v, velum.

individual filaments (Fig. 2*b*) were cylindrical, covered with an external limiting membrane (elm, Fig. 2*b*) and measured 1 mm in diameter. Within this diameter, four to five egg capsules were found. Egg capsules (hc, Fig. 2*b*) measured about .280 mm in diameter and the zygotes (z, Fig. 2*b*), .138 mm in diameter. There were approximately 500 egg capsules per centimeter of filament and the whole egg mass was estimated to contain 66,000 eggs. Egg capsules did not appear to touch each other and there were thin membranous transparent

FIG. 1. Diagrammatic representation of pallial portion of female genital duct in *Cerithium nodulosum*. ag, albumen gland; ars, aperture of receptaculum seminis; bc, bursa copulatrix; cg, capsule gland; cm, columellar muscle; ct, ciliated tube; ga, glandular area; ll, latteral lamina; me, mantle edge; ml, medial lamina; o, oviduct; og, oviducal groove; rs, receptaculum seminis; scg, sperm collecting gutter; sn, snout; t, tentacle. Arrows represent ciliary currents.

strands which often appeared between them. The eggs and zygotes were moderately telolecithal and cleavage was unequal. Blastulation occurred rapidly within 5 hours of deposition. Depending upon their position in the egg mass, some zygotes were already undergoing cleavage and blastulation by the time oviposition had ceased. Gastrulation was also rapid and appeared to occur by epiboly. Within 24 hours early larval stages were present and revolving within their individual hyaline capsules. A day later larvae attained a recognizable veliger stage. Veligers have a well-defined bilobed velum covered with compound cilia (v, Fig. 2*c*). The shell is tan colored, caplike and large, and covers the digestive anlage (da, Fig. 2*c*). A prominent ciliated foot (f, Fig. 2*c*) and operculum (op, Fig. 2*c*) were also evident, and the veligers continued to revolve in their capsules. At the end of two days, eye spots and statocysts (st, Fig. 2*c*) were seen and the shell had a definite coil to it. Hatching took place in 3 days but varied according to the position of the egg in the egg mass. The egg capsule appeared to collapse due to the ciliary beat of the velum and the emerging free-swimming veligers appeared to have lost their compound cilia; they were rapid swimmers and darted about quickly. The embryonic shells were brown and lightly pitted. The operculum was unusually large in comparison to observations made on opercula of other *Cerithium* species. Free-swimming veligers were maintained in aquaria for 3 days after hatching but died thereafter. The length of their planktonic life remains unknown.

DISCUSSION

The anatomy of the reproductive tract of *C. nodulosum* is similar to other *Cerithium* species examined from Eniwetok and appears to be representative of the cerithiids as a group. My present work on the genus in Florida and the Caribbean generally confirms the fact that both male and female reproductive tracts are open in the pallial region and follow the general pattern described by Johansson (1954) for the Cerithiaceae. The open gonadal ducts of *Cerithium* are similar to those described for the closely related genera *Bittium* (Johansson, 1947; Fretter and Graham, 1961), *Cerithiopsis* (Fretter, 1951), and *Tympanotonus* (Johnansson, 1954). They also resemble those described for pleurocerids by Dazo (1965). Johansson's (1954) interpretation of the function of the chamber located in the outer portion of the medial lamina as a bursa copulatrix is probably correct; however, the glandular area and its opening in the wall of the bursa were not mentioned by him. I have found it in all members of the genus that I have examined. It may serve as an auxiliary receptaculum seminis prior to fertilization. The location of the receptaculum seminis near the distal portion of the gonadal duct is puzzling. Sperm leaving the bursa may travel down the gonadal duct and be initially stored there. Then, during oviposition, they may leave it and again enter the sperm-collecting gutter, ciliated tube, and bursa, to be eventually stored in the glandular area of the bursa prior to fertilization. Oriented sperm have been seen in this glandular area, but no sectioning was done and such a function remains unconfirmed.

The egg mass of *Cerithium nodulosum* differs from other cerithiid spawns in the thick axial base by which it is attached to the substrate. Otherwise the filaments of the mass are quite typical for the group. Development is also similar to that described for other species of *Cerithium* which have planktonic life stages.

LITERATURE CITED

ANDERSON, D. T. 1960. The life histories of marine prosobranch gastropods. Journal of the Malacological Society of Australia, no. 4, pp. 16–29.

D'ASARO, C. 1965. Development of *Strombus gigas*. Bulletin of Marine Science, vol. 15, no. 2, pp. 359–416.

——— 1970. Egg capsules of prosobranch mollusks from South Florida and the Bahamas and notes on spawning in the laboratory. Bulletin of Marine Science, vol. 20, no. 2, pp. 414–440.

DAVIS, C. C. 1967. Emergence of veliger larvae from eggs in gelatinous masses laid by some Jamaican marine gastropods. Malacologia, vol. 5, no. 2, pp. 299–308.

DAZO, B. C. 1965. The morphology and natural

history of *Pleurocera acuta* and *Goniobasis livescens* (Gastropoda: Cerithiacea: Pleuroceridae). Malacologia, vol. 3, no. 1, pp. 1–80.

DEMOND, J. 1957. Micronesian reef-associated gastropods. Pacific Science, vol. 11, no. 3, pp. 275–341.

FRETTER, V. 1951. Observations on the life history and functional morphology of *Cerithiopsis tubercularis* and *Triphora perversa.* Journal of the Marine Biological Association of the United Kingdom, vol. 29, pp. 567–586.

FRETTER, V., and A. GRAHAM. 1962. British prosobranch mollusks. Ray Society, London. 755 pp.

JOHANNSON, J. 1947. Über den offenen Uterus bei einigen Monotocardiern ohne Kopulationsorgan. Zoologiska bidrag fron Uppsala, vol. 25, pp. 102–110.

——— 1953. On the genital organs of some mesogastropods: *Cerithium vulgatum*, Brug., *Triphora perversa* (L.) and *Melanella* (*Eulima*) *intermedia* (Cantr.). Contributions to the phylogeny of the pallial gonoducts of the prosobranchia. Zoologiska bidrag fron Uppsala, vol. 30, pp. 1–23.

——— 1954. On the anatomy of *Tympanotonus fuscatus* including a survey of the open pallial oviducts of the Cerithiaceae. Atlantidae Report, vol. 4, pp. 149–166.

LEBOUR, M. V. 1945. The eggs and larvae of some prosobranchs from Bermuda. Proceedings of the Zoological Society of London, vol. 114, pp. 462–489.

LOBIANCO, S. 1888. Notizie biologiche riguardanti specialmente il periodo di maturita sessuale degli animali del golfo di Napoli. Mittheilungen an der Zoologischen Station zu Neapel (Leipzig), vol. 8, pp. 385–440.

MARCUS, E., and E. MARCUS. 1964. On *Cerithium atratum* (Born 1778) (Gastropoda: Prosobranchia). Bulletin of Marine Science of the Gulf and Caribbean, vol. 14, no. 3, pp. 494–510.

NATARAJAN, A. V. 1958. Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and the Palk Bay. Proceedings of the Indian Academy of Sciences, vol. 46, pp. 170–228.

OSTERGAARD, J. M. 1950. Spawning and development of some Hawaiian marine gastropods. Pacific Science, vol. 4, no. 2, pp. 75–115.

RAEIHLE, D. 1968. Notes on captive *Cerithium variabile* and *Mitra floridana.* Annual Report of the American Malacological Union, Inc. for 1968, pp. 35–36.

RISBEC, J. 1943. Recherches anatomiques sur les prosobranches de Nouvelle-Caledonie. Annales des Sciences Naturelles, Zoologie, series 11, vol. 5, pp. 89–112.

ROBERTSON, R. 1959. Observations on the spawn and veligers of conchs (*Strombus*) in the Bahamas. Proceedings of the Malacological Society of London, vol. 33, no. 4, pp. 164–172.

SUNDERBRINK, O. 1929. Zur Frage der Verwandtschaft zwischen Melaniiden und Cerithiiden. Zeitschrift für Morphologie und mikroskopische Anatomie, vol. 14, pp. 261–337.

WOLFSON, F. H. 1969. Spawning notes IV: *Cerithium stercusmuscarum.* Veliger, vol. 11, no. 4, pp. 441–442.